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No. 8 — *The Relationships Of Four Small Hispaniolan* Eleutherodactylus (*Leptodactylidae*)

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Perhaps the most confusing group of the genus *Eleutherodactylus* in the West Indies is that composed of the small to minute frogs of Hispaniola, none of which has a snout-vent length in excess of 25 mm. To this assemblage belong *E. minutus* Noble 1923, *E. abbotti* Cochran 1923, *E. audanti* Cochran 1934, and *E. haitianus* Barbour 1942 (= *E. intermedius* Cochran 1941, preoccupied). *E. abbotti* was described from Laguna, Samaná Province, República Dominicana, *E. audanti* from Peak la Selle (= Mont la Selle), Dept. de l'Ouest, Haiti. The remaining two forms were described from the interior uplands of the Cordillera Central in La Vega Province (República Dominicana), *minutus* from near Paso Bajito, Jarabacoa-Constanza Trail, and *haitianus* from Loma Rucilla, 8000 to 10,000 feet. Although *minutus* and *haitianus* are still known only from various localities in the Cordillera, *abbotti* has been reported from many localities in the República Dominicana and Haiti. *E. audanti* is here reported for the first time from outside of the Massif de la Selle.

Shreve and Williams (1963: 320–323) discussed at some length the situation of the species *audanti* and *abbotti* in the Port-au-Prince region. Conclusions drawn from my own experience in the field in both Haiti and the República Dominicana in 1962 and 1963 differ from theirs, and are drawn in part from a large body of fresh material from critical localities both outside and within the range of their particular study.

Through the courtesy and cooperation of the following curators, I have been able to study specimens of this group of frogs: Ernest E. Williams, Museum of Comparative Zoology (MCZ); Doris M. Cochran, United States National Museum (USNM); and Charles M. Bogert and Margaret Bullitt, American Museum of Natural History (AMNH). Specimens in my own collection are designated Albert Schwartz Field Series (ASFS). In the field in Hispaniola I had the capable assistance of Patricia A. Heinlein and Ronald F. Klinikowski, Dennis R. Paulson, David C. Leber, and Richard Thomas. To all of them I express my sincere thanks for their interest in these small frogs. The illustrations for the present paper are the work of Klinikowski and Leber; they again merit my gratitude for their endeavors.

ELEUTHERODACTYLUS ABBOTTI AND *ELEUTHERODACTYLUS AUDANTI* ON THE SOUTH ISLAND[1]

Although *E. abbotti* was known from the south island by only two doubtfully identified specimens (from Pétionville and Fond-des-Nègres, Haiti) at the time of Cochran's monograph on the herpetology of Hispaniola (1941), it is now known from many localities there.

Shreve and Williams (1963) in a study of a large number of small frogs from the La Selle region presented the following conclusions: 1) *audanti* is a subspecies of *abbotti* because "of the presence in the lowlands of the Port-au-Prince region and on the southwest peninsula and in Barahona of equivocal specimens which appear to be in various grades and degrees intermediate between *audanti* and *abbotti*"; 2) there are no absolute differences between these two species; 3) at intermediate levels north of the Massif de La Selle, such as Furcy, there exist populations of frogs, some of which may be identified as *abbotti*, others as *audanti*, and still others intermediate between these two species; and 4) material from various lowland and highland localities (Península de Barahona, Morne de Cayette, Pétionville, Fond-des-Nègres, Thiotte) cannot be referred with certainty to either *abbotti* or *audanti* and are considered to be intergrades. An interesting sidelight on Shreve and Williams' study was the discovery of "the presence in the foothills of the La Hotte region . . . of frogs much more like *abbotti* than any others in the area south of the Cul de Sac Plain." This analysis would suggest that *abbotti* and *audanti* are conspecific, and that *audanti* is restricted to the highest peaks of the La Selle, intergrades with *abbotti* at lower levels, and is replaced by *abbotti* in the lowlands.

However, while collecting at Furcy in the summer of 1962, it quickly became obvious that we were dealing with two types of small frogs. Both are vocally very similar; the call of each is a series of highpitched "tuck" 's, followed by a sharply ascending "wheep" (although a series of "tuck-wheep, tuck-wheep" 's may be interspersed in the normal call series, usually at its end or beginning). The call of the smaller of these two frogs (*audanti*) was distinctly higher than that of the larger (*abbotti*), but otherwise the calls were identical in structure. However, these two forms differ markedly from one another in that *abbotti* has a

[1] The terms "south island" and "north island" are used in this paper as, for example, by Williams, 1961.

grayish green to tan ground color, is without definite leg bars and postanal triangle (Fig. 1, left), and has an all yellow venter, whereas *audanti* has a much more brightly colored dorsum, most often some shade of reddish brown or buff, with a distinct and clear-cut postanal triangle and leg bars (Fig. 1, right), and a gray belly which is often spotted.

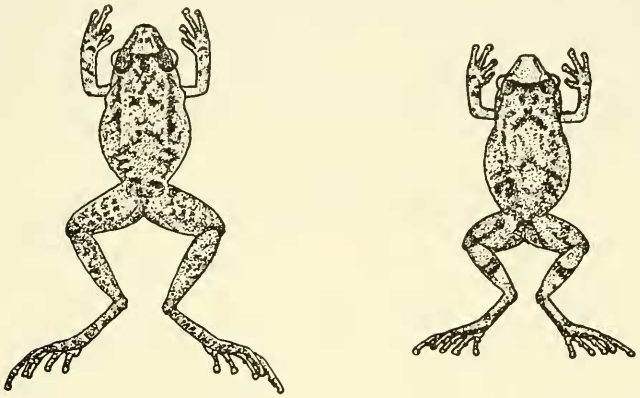

FIG. 1. *Left: Eleutherodactylus abbotti*, adult female, ASFS X1649, Furcy, 5600′, Dépt. de l'Ouest, Haiti; snout-vent length 23.0 mm.
Right: Eleutherodactylus audanti audanti, adult female, ASFS X2362, 2.4 mi. S Kenscoff, Dépt. de l'Ouest, Haiti; snout-vent length 23.3 mm.

All the preserved specimens of these frogs collected by others in the Furcy area can be separated into these two categories without difficulty. Naturally, the yellow ventral coloration is no longer present; the distinct leg and postanal markings of *audanti* remain, however, and these are a ready means of differentiation between the two species. Occasional "intermediates" (i.e., *audanti* with slightly less clear-cut postanal triangle or *abbotti* with more definite leg bands) I consider to be within the natural range of variation of each of the two species involved; the Furcy population is in no way composed of a large number of intergrades with *abbotti* and *audanti* at the two extremes. It is, rather, composed of frogs which are readily assignable to either *audanti* or *abbotti* on the basis of pattern, with a very occasional specimen of each whose markings slightly resemble those of the other species in degree of clarity. Thus, at least at Furcy, *audanti* and *abbotti* appear not as two races of one form, but as two sympatric species.

The following table (Table I) is based on a selection of ten

specimens of each sex of each species (using as the criterion for species the pattern described above) from the south island Haitian uplands. These series include the largest member of each sex in each case, and the type (a female) of *audanti*, as well as three other adult female paratypes. Measurements and ratios indicate the following: in males, *abbotti* reaches a larger size than *audanti* (in females, the reverse appears to be true, but this is apparently an artifact of the *abbotti* sample, since there are female *abbotti* from medium elevations in the Cordillera Central which have a snout-vent length equal to that of the largest *audanti*); measurements of femur, tibia, and fourth toe are diagnostic, as is the tibia/snout-vent ratio.

TABLE I[1]
(measurements in millimeters)

	Snout-vent length (maximum)	Tibia		Femur		Tibia/snout-vent ratio	
		range	aver-age	range	aver-age	range	aver-age
abbotti ♂	19.3	8.8–10.1	9.3	7.7– 8.5	8.0	48.6–55.4	52.2
audanti ♂	18.4	7.2– 8.0	7.6	6.1– 7.0	6.6	40.8–46.8	43.8
abbotti ♀	23.6	11.1–13.0	11.9	9.7–11.4	10.2	50.4–56.6	53.5
audanti ♀	25.3	9.0–10.8	10.1	8.0– 9.8	9.1	38.6–47.1	43.6

The following additional descriptive notes on the patterns of the two species should be helpful. *E. audanti* is well illustrated by Cochran (1941: 66). The heavily and distinctly crossbarred limbs and the dark postanal triangle are clearly shown. The leg bars — one on the crus, one on the pes, and two incomplete bars on the thigh — are usually outlined in preserved material by pale bands, which set the bars off very distinctly from the ground color. There is a single bar on the antebrachium, and another on the wrist, again outlined by pale color. The dorsal pattern may have a middorsal stripe. The major feature of the dorsal pattern is a scapular X, the anterior limbs of which are usually fused to the dark interocular bar; often the area between the interocular bar and the anterior arms of the X is likewise dark, thus giving a

[1] Head measurements, not included in the table, are less clear-cut. In males all these measurements overlap greatly, although *abbotti* averages consistently higher. In females, *abbotti* averages larger in head length (8.2 vs. 8.1) and naris to eye (2.4 vs. 2.2), but slightly less in head width (8.4 vs. 8.5) and diameter of tympanum (1.4 vs. 1.5); diameter of eye averages the same in both species (3.0), although the eye of *abbotti* reaches a larger maximum size. In no head measurements are the females of the two species separable.

rather complex occipital and scapular figure. The sides may be dark like the back, or may have a series of about five horizontal bars before the groin. Two fresh specimens have a tan dorsal band from snout to vent, with darker brown sides, the scapular X faint but still present. The ventral dark pigmentation is variable, but always present; there may be stippling, mottling, or even blotching on the throat and belly; the underside of the hindlimbs is always heavily stippled with brown. The pale snout of *audanti* is a characteristic of the species.

E. abbotti, on the other hand, is generally paler than *audanti* when preserved, and although it has the scapular X which is joined to the interocular bar, the same number of limb bands as *audanti*, and even, at times, has the vertical side stripes, none of the features is so bold and diagrammatic as in *audanti*. The entire dorsal surface is irregularly mottled with darker color, and the individual pattern elements are lost in the general obliterative effect of the dorsal pigmentation. There is no clear-cut postanal triangle, although the postanal area is somewhat darker than the rest of the concealed surfaces. The limb bars are not set off from the ground color by a distinct pale area; in fact, they have been so much invaded by pale color that they are no longer conspicuous. Usually the ventral surfaces are almost immaculate, although there may be some diffuse stippling on the throat, and an occasional individual has some belly stippling.

Cochran (1941: 67–68) has described in great detail the pallid dorsal coloration and asymmetrical spotting which occur in some specimens of *audanti*. Apparently the entire dorsum loses its basic pattern, and a blotchy, irregular, asymmetrical pattern is superimposed upon the now unicolor back, so that the preserved specimen is pale, variously and irregularly mottled with dark brown. Of the large series from Furcy available, only two individuals show this mottling, and even in them it is apparently in its earliest stages. The back of one still retains some semblance of pattern, but there are large licheniform patches on the hindlimbs. The other is uniform pale pinkish dorsally, but the hindlegs show expansion of the dark pigment from the crural bands and elsewhere on the legs. This irregularly mottled state is more common in specimens from the high La Selle, where large numbers in any given series may be mottled. The faded back and increased mottling is not a condition of age, since some tiny juveniles, as well as adult and subadult males and females all show the mottled state. Invariably, from any single locality, there are both "normal" and mottled individuals in the sample.

Shreve and Williams (1963: 322) stated that "nothing . . . comparable to the orange or asymmetrically pigmented specimens of *audanti* occurs in the *abbotti* populations north of the Cul de Sac." However, there is a single specimen of *abbotti* from the lowlands near Pimentel in the República Dominicana (and thus well outside the range of *audanti*) which clearly shows this condition. In addition, there are frogs (for example, one from Furcy, MCZ 33549, one from Savane Zombi, MCZ 31953, and two from 10.5 miles south of Cabral, ASFS V71 and V83) which are typical *abbotti* in size, proportion, and residual pattern, and show no *audanti* influence in these respects, but which, nevertheless, have the mottled condition of *audanti*. These could, perhaps, be considered intergrades. However, there are typical *abbotti* available from the same localities, and, of the three localities, only at Furcy do the two species occur together. Since *abbotti*, when far outside *audanti* genetic influence, may manifest this sort of peculiar spotting, I regard these specimens as within the chromatic variation of *abbotti*.

Since *audanti* and *abbotti* are members of the *auriculatus* group, both have external vocal sacs, granular bellies, small patch-like vomerine teeth, and enlarged digital discs. I am unable to distinguish the two species on any structural basis; one possibility is that the vomerine teeth of *abbotti* are slightly more oblique than those of *audanti*, but this is at best a very subjective character. Like most members of the *auriculatus* group, both *audanti* and *abbotti* lack inguinal glands.

E. audanti is known from near the Dominico-Haitian border (Forêt des Pins) west to the vicinity of Pic Macaya (foothills, Massif de la Hotte). It is restricted to the uplands — the lowest locality whose altitude is known and whence *audanti* has been collected is Peneau, 5000 feet. A possibly lower locality is 2.4 miles south of Kenscoff, but no altitude is available. The highest locality is Mont Cabaio (7000 feet), although specimens are recorded from Mont la Selle, without elevation given (the summit of Mont la Selle is slightly over 8000 feet). The specimens from Pic Macaya (MCZ 21551–53) represent the only Haitian *audanti* outside of the Massif de la Selle; they do not differ in pattern from La Selle specimens. The adult female of the series has a tibia/snout-vent ratio of 48.9, slightly greater than that reported above for La Selle frogs.

In the La Selle region, *abbotti* occurs with *audanti* at elevations up to 5600 feet (Peneau, Furcy, 2.4 miles south of Kenscoff). There are specimens of *abbotti* from Savane Zombi (4200 feet) but

none from Forêt des Pins at 5800 feet where *audanti* has been collected. *E. abbotti* has also been collected from the lower southern slopes of the La Selle (one specimen, Thiotte, about 3000 feet); from the northern lowlands of the eastern Tiburon Peninsula (one specimen, Morne de Cayette); from the western extremity of the Tiburon, both north (one specimen, Marfranc, 120 feet) and south (eight specimens, Camp Perrin, 1000 feet) of the Massif de la Hotte; and from the intermediate southern slopes of this range (five specimens, Carrefour Canon, 500 feet). (See Fig. 5 for distribution of these two species.)

A large amount of fresh material from the Península de Barahona and the Sierra de Baoruco indicates that *abbotti* occurs there as well. In this region it has been taken from near sea level (La Ciénaga) up to 3700 feet in the Sierra de Baoruco. In fact, *abbotti* is the dominant small frog in this entire region. The absence of *audanti* from the Sierra de Baoruco may be more apparent than real. Since *audanti* in the La Selle has not been taken lower than about 5000 feet, it may well not occur at lower elevations in the Sierra de Baoruco. Most collecting in these mountains has been in the Valle de Polo region, whose elevation is less than that for the lowest record of *audanti* to the west.

In summary, *E. abbotti* is widespread throughout the south island, occurring from about sea level to elevations of 5600 feet. The species occurs not only in the lowlands, but in the La Hotte-La Selle-Baoruco massif up to moderate elevations. *E. audanti*, on the other hand, is known only from elevations above 5000 feet in the massifs de la Hotte and la Selle, and in the latter range is extremely abundant at these higher elevations. Its occurrence on the Sierra de Baoruco requires confirmation.[1] Both species occur together at elevations between 5000 and 5600 feet, at least in the Massif de la Selle.

[1] Since the above was written, David C. Leber and Richard Thomas, in the summer of 1964, succeeded in securing *E. audanti* in the Sierra de Baoruco. Near the Dominico-Haitian border, eleven specimens of *audanti* were secured between 4 and 11 kilometers northeast of Los Arroyos, Pedernales Province, at elevations between 5600 feet and 7200 feet. In this same general region, nine specimens of *E. abbotti* were also collected; these are from six localities ranging in elevation from 2200 feet to 5800 feet. The latter high elevation gives an increase of altitudinal overlap between *audanti* and *abbotti* of 200 feet in the southern massifs. At one locality (5 km NE Los Arroyos) both species were collected together. These new localities are not included on the map, nor are these specimens included in the computations.

ELEUTHERODACTYLUS ABBOTTI AND *ELEUTHERODACTYLUS AUDANTI* ON THE NORTH ISLAND

E. abbotti has long been known to occur throughout much of the north island. Described from Laguna on the Península de Samaná, this frog was subsequently reported from many localities in the República Dominicana (Cochran, 1941; Mertens, 1939), from the Dominico-Haitian border east to the Península de Samaná and the south shore of the Bahía de Samaná. Its distribution in Haiti is poorly known; it has been reported only from near Limbé (Lynn, 1958), the Citadelle (Cochran, 1941: 61), and Grande Rivière (Shreve and Williams, 1963: 322). The relatively small number of specimens of *abbotti* in collections prompted Shreve and Williams to suggest that *abbotti* was "nowhere very abundant." On the contrary, *abbotti* is an extremely abundant frog, somewhat more so in the uplands than in the lowlands. Not only can it be collected at night, when huge choruses make the forest resound, but can often be secured with ease during the day in piles of coconut trash and old, rotting, and very wet piles of cacao husks.

In the Cordillera Central *abbotti* occurs up to elevations of 6000 feet (Loma Vieja; 9.1 miles north of Constanza; 9.3 miles north of Constanza). In the Sierra de Neiba it occurs at elevations as high as 5000 feet (14.5 miles south of Elías Piña). The Cordillera elevation is slightly in excess of the highest known records in the Massif de la Selle, but not strikingly so. The altitude of major abundance in the Cordillera is apparently about 3600–4000 feet, where *abbotti* forms the largest portion of nocturnal frog choruses in broadleaf gallery forest along rivers in pinewoods.

The measurements of three series of *abbotti* (ten males and ten females each) from southern Haiti (La Selle), the interior Dominican uplands (Cordillera), and northern República Dominicana are tabulated below (Table II) and reveal certain differences among them. (Each series included the largest members of both sexes; in each series most females were gravid.)

In coloration and pattern there appear to be no differences among the various populations studied. The typical dorsal ground color varies from gray to some shade of tan or light brown; there is a dark interocular bar, crossbars on the limbs, a yellowish to whitish-gray belly, and a yellow vocal sac. Despite its wide geographic and altitudinal distribution, *abbotti* has apparently not differentiated into races.

TABLE II. Means and extremes of nine measurements and one ratio in three populations of *Eleutherodactylus abbotti* consisting of the ten largest specimens of each sex from each region. (No races are recognized.)

	Haitian uplands	República Dominicana uplands	northern República Dominicana
	10♂	10♂	10♂
snout-vent length	17.9 (16.4–19.3)	18.5 (17.9–18.9)	17.8 (17.0–18.8)
head length	6.5 (6.1– 7.0)	6.4 (6.0– 6.9)	6.4 (6.0– 6.8)
head width	6.6 (6.0– 7.1)	6.5 (6.3– 7.3)	6.6 (6.0– 7.4)
tympanum	1.3 (1.1– 1.4)	1.2 (1.0– 1.3)	1.2 (1.0– 1.5)
eye	2.6 (2.5– 2.7)	2.4 (2.2– 2.6)	2.7 (2.3– 3.0)
naris to eye	1.8 (1.6– 2.0)	1.9 (1.7– 2.0)	1.8 (1.7– 2.0)
femur	8.0 (7.7– 8.5)	7.7 (7.1– 8.3)	7.8 (7.5– 8.2)
tibia	9.3 (8.8–10.1)	8.8 (8.5– 9.3)	8.8 (8.5– 9.3)
fourth toe	8.3 (7.5– 9.3)	7.6 (6.6– 8.1)	7.5 (7.0– 7.8)
tibia/snout-vent ratio	43.8 (40.8–46.8)	47.9 (45.5–51.1)	50.0 (45.7–52.5)
	10♀	10♀	10♀
snout-vent length	22.2 (20.9–23.6)	22.7 (20.4–25.4)	21.4 (20.9–22.8)
head length	8.2 (7.4– 9.3)	8.1 (7.1– 8.8)	7.8 (7.5– 8.4)
head width	8.4 (7.9– 9.2)	8.1 (6.9– 9.6)	7.9 (7.5– 8.7)
tympanum	1.4 (1.3– 1.6)	1.5 (1.2– 1.7)	1.4 (1.2– 1.6)
eye	3.0 (2.8– 3.4)	2.9 (2.5– 3.4)	3.0 (2.8– 3.2)
naris to eye	2.4 (2.0– 2.8)	2.3 (1.8– 2.6)	2.3 (2.1– 2.7)
femur	10.2 (9.7–11.4)	9.9 (8.6–10.8)	9.1 (8.3– 9.8)
tibia	11.9 (11.1–13.0)	11.1 (9.7–12.5)	10.5 (9.9–11.2)
fourth toe	10.3 (9.0–11.3)	9.4 (7.9–10.6)	8.8 (8.2– 9.7)
tibia/snout-vent ratio	53.5 (50.4–56.5)	48.9 (45.6–51.3)	49.2 (47.2–51.9)

Two samples of small frogs, from the Sierra de Neiba and the Cordillera Central, merit special attention. The series from the Sierra de Neiba consists of nine frogs from three localities ranging in elevation from 4750 feet to 5950 feet; there are eight adult males and one juvenile. The Cordillera series is made up of nine adult male frogs taken while calling; the elevation for part of this lot is 5000 feet (Valle de Culata). The specimens from 4 miles (7 km) north of Constanza have no recorded elevation, but are from above 5000 feet. These two small series are distinctly different from *abbotti* and are quite like *audanti* from the Massif de la Selle. The bold postanal triangle and the conspicuously banded limbs ally these small frogs with *audanti;* all are from high elevations. The voice of the Cordillera specimens resembled the high-pitched calls

of *audanti* more than the lower calls of *abbotti*. At Valle de Culata these *audanti* and *abbotti* were heard calling in the same abandoned field, which was grown up in *Pteris* and blackberries. The call of *audanti* at this locality reminded me very distinctly of that of *E. auriculatus* in Cuba — a long series of telegraphic clicks (= "tucks") with an occasional, almost inaudible "wheep" at the end of the series. The *abbotti* call at this locality was that typical for the species throughout its range, and was quite obviously different from the call of *audanti*.

It is remarkable that, despite the large number of frogs which have been collected from the Cordillera Central, *audanti* is presently known only from the Valle de Culata region. This valley is not especially distinctive, being rather small and mostly cut over or burned for pasture.

E. audanti is an upland species, with apparently isolated populations; the Sierra de Neiba and Cordillera populations differ not only from one another but also from the La Selle form. For the Sierra de Neiba population I propose the name:

Eleutherodactylus audanti notidodes [1] new subspecies

Holotype. MCZ 43204, an adult male, from 20 km (11.7 miles) southwest Hondo Valle, elevation 5950 ft., Independencia Province, República Dominicana, one of a series taken 11 August 1963 by David C. Leber and Richard Thomas. Original number ASFS V371.

Paratypes. ASFS V372–74, AMNH 71990–92, same data as type; ASFS V385, 14.5 km (8.4 miles) SW Hondo Valle, 4750 ft., San Rafael Province, República Dominicana, 11 August 1963, R. Thomas; MCZ 43205, 25 km (14.5 miles) S Elías Pina, 5000 ft., San Rafael Province, República Dominicana, 17 August 1963, A. Schwartz.

Diagnosis. A subspecies of *E. audanti* characterized (in males; females unknown) by larger size than *a. audanti* (male *a. audanti* to 18.4 mm, male *a. notidodes* to 21.9), longer hind legs, ratio of tibia/snout-vent length higher (46.5 in *notidodes*, 43.8 in *audanti*), little or no dark ventral pigmentation, and hind leg crossbars distinct but not prominently set off from ground color by pale outlining.

Description of type. An adult male with the following measurements (in mm) and ratio: snout-vent length, 21.9; head length, 7.5;

[1] From the Greek *notis, notidis*, moisture, wet, and *-odes*, dweller.

head width, 7.4; diameter of tympanum, 1.2; diameter of eye, 2.7; naris to eye, 2.2; femur, 7.9; tibia, 10.1; fourth toe, 8.6; tibia/snout-vent length, 46.1. Head width equal to head length; snout truncate with nares conspicuous at anterior end of canthus rostralis; diameter of eye greater than distance from naris to anterior corner of eye; interorbital space 2.6, about equal to diameter of eye; diameter of tympanum much less than diameter of eye, distance from tympanum to eye equal to about three-quarters diameter of tympanum. Digital discs present, that of digit three the largest and equal to about two-thirds area of tympanum. Fingers moderate in length, unwebbed, 3–4–2–1 in order of decreasing length; subarticular tubercles well developed, pale gray. Toes moderate in length, unwebbed, 4–3–5–2–1 in order of decreasing length; subarticular tubercles dark gray and prominent. Heels touch when femora are held at right angles to body axis. Dorsum finely warty or shagreened with a raised median line from snout to above vent. Throat and belly granular; vocal sac present, large, extending posteriorly to between forelimbs, heavily glandular anteriorly. Inguinal glands absent. Posterior surface of thighs with large juxtaposed rounded granules. Tongue small, oval, entire, free behind, its greatest width about one-half that of floor of mouth. Vomerine teeth in two sharply oblique patches, beginning within the median border of the choanae, and separated from the choanae by a distance equal to slightly less than the diameter of a choana, and from each other by a distance equal to the length of one tooth row.

Coloration of type in life. Dorsal ground color tan with a darker brown interocular bar and a scapular X; snout, anterior to interocular bar, slightly paler than back; area between interocular bar and two anterior arms of X suffused with darker brown; back in general rather uniformly tan, but on the sides this breaks down into a series of about four lateral bars, separated from one another by creamy gray from the belly. Hindlimbs tan with two crossbars on the thigh, neither especially prominent and neither outlined with pale color; a more conspicuous crural cross-bar, vaguely outlined with pale color; and a single cross-bar on the pes. Forelimbs with one antebrachial bar and a wrist bar. A prominent dark bar from the snout through the eye to the forelimb insertion and covering the upper half of the tympanum. A prominent and very dark brown postanal triangle, extending onto the underside of the thighs. Ventral ground color creamy gray with scattered dark brown stippling, most concentrated on the vocal sac and undersides of the limbs. Iris silvery above.

Variation. Variation in measurements and ratios is shown in Table III. Structurally all the paratypes resemble the type. The rather widely separated vomerine teeth and the angulated arrangement of the two series in relationship to one another are common features.

TABLE III. Means and extremes of three populations of *Eleutherodactylus audanti*. (Females unknown from Sierra de Neiba and Cordillera Central. Sample from Haiti consists of the ten largest specimens of each sex.)

	E. a. audanti [Haitian uplands]	*E. a. notidodes* [Sierra de Neiba]	*E. a. melatrigonum* [Cordillera Central]
	10♂	8♂	9♂
snout-vent length	17.4 (16.2–18.4)	19.9 (17.9–21.9)	18.2 (17.6–20.3)
head length	6.1 (5.7– 6.4)	7.0 (6.5– 7.5)	6.5 (6.0– 6.9)
head width	6.3 (5.8– 6.6)	7.3 (6.3– 7.9)	6.6 (6.1– 7.3)
tympanum	1.1 (0.9– 1.3)	1.2 (1.0– 1.4)	1.2 (0.9– 1.4)
eye	2.4 (2.2– 2.5)	2.8 (2.4– 3.1)	2.6 (2.0– 3.0)
naris to eye	1.7 (1.5– 1.8)	2.2 (2.0– 2.4)	1.9 (1.6– 2.2)
femur	6.6 (6.1– 7.0)	7.7 (6.9– 8.5)	7.2 (6.4– 8.0)
tibia	7.6 (7.2– 8.0)	9.9 (8.4–10.1)	8.2 (7.8– 8.5)
fourth toe	6.6 (5.9– 7.1)	8.0 (7.2– 8.6)	7.0 (6.6– 7.5)
tibia/snout-vent ratio	43.8 (40.8–46.8)	46.5 (44.7–48.3)	45.0 (40.9–47.4)
	10♀		
snout-vent length	23.1 (22.1–25.3)		
head length	8.1 (7.4– 8.6)		
head width	8.5 (7.3– 9.2)		
tympanum	1.5 (1.2– 1.6)		
eye	3.0 (2.7– 3.2)		
naris to eye	2.2 (2.0– 2.4)		
femur	9.1 (8.0– 9.8)		
tibia	10.1 (9.0–10.8)		
fourth toe	9.2 (8.4– 9.8)		
tibia/snout-vent ratio	43.6 (38.6–47.1)		

In coloration, the paratypes are quite variable. All but one were tan in life, but only a single specimen has the rather uniform dorsal pigmentation of the type. In all, the leg bars are more prominent than in the type, although never outlined boldly with paler color. Five specimens have a dark tan dorsum, somewhat irregularly pigmented, with a vague pair of pale reversed parentheses, dark interocular bar, scapular X, and pale snouts. Only one of these normally colored specimens has any indication of ventral mottling, and this is sparse and confined to the sides of

the abdomen. All the other individuals have only faint dark stippling ventrally. Two males have a pinkish orange dorsum with irregular dark brown mottling on the limbs, sides, sacrum, and head — the typical asymmetrical *audanti* pattern described in detail by Cochran. Their dorsal blotching carries over onto the venter, but is not heavy there. The smallest paratype (snout-vent 11.1 mm) is pale pink, with prominent limb bars, but with no irregular dark mottling.

Comparisons. *E. a. notidodes* requires comparison both with the nominate race and with *E. abbotti*, which occurs with it. Compared with *a. audanti*, *notidodes* reaches a larger size, and averages greater in all measurements. There is virtually no overlap of extremes in measurements of head length, eye, naris to eye, femur, tibia, and fourth toe. *E. a. notidodes* has a longer tibia than does *a. audanti*, although the overlap of the ratios is great. Both subspecies are much alike in coloration and pattern; both show some individuals with asymmetrically blotched dorsal pigmentation. Both have a dark postanal triangle and both show dark limb bars, although those of *notidodes* are not outlined in paler color. The ventral pigmentation is much heavier in *a. audanti*; the *notidodes* with the heaviest ventral pigmentation is lighter than the most lightly pigmented *audanti*.

Compared with male *abbotti* from the interior highlands, male *notidodes* reach a larger size (21.9 vs. 18.9) and are longer snouted (naris to eye 2.2 [2.0–2.4] in *notidodes*, 1.9 [1.7–2.0] in *abbotti*). All other measurements show a great deal of overlap, although *notidodes* averages higher in every measurement except tympanum diameter (1.2 in both species) and femur (7.7 in both species). The tibia/snout-vent length ratio averages greater (47.9) in *abbotti* than in *notidodes* (46.5). None of these measurements is so helpful as pattern for differentiating the two species; by means of the brown postanal triangle and the heavily banded legs, they can be distinguished without difficulty.

The vomerine teeth may prove to be useful in differentiating the two subspecies of *E. audanti*. The teeth in *a. audanti*, although patch-like, seem to be arranged more horizontally than the series in *notidodes*; in the latter subspecies the patches appear to be more diagonal, the two series directed toward one another posteriorly in a broad V.

The small series of *E. audanti* from the Constanza region in the Cordillera Central may be known as:

ELEUTHERODACTYLUS AUDANTI MELATRIGONUM[1] new subspecies

Holotype. MCZ 43206, from 7 km (4 miles) north of Constanza, La Vega Province, República Dominicana, one of a series taken 7 July 1963, by David C. Leber and Richard Thomas. Original number ASFS X8774.

Paratypes. ASFS X8773, X8775–77, same data as type; AMNH 71993–96, 5.1 miles north of Constanza, Valle de Culata, 5000 ft., La Vega Prov., República Dominicana, 8 July 1963, D. C. Leber, R. Thomas.

Diagnosis. A subspecies of *E. audanti* characterized (in males; females unknown) by moderate size (male *a. audanti* to 18.4, *notidodes* to 21.9, *melatrigonum* to 20.3 mm), intermediate length of tibia, hindleg crossbars distinct and variously outlined in paler color, although never so boldly as in *a. audanti*, and pinkish belly with scattered dark chromatophores.

Description of type. An adult male with the following measurements and ratio: snout-vent length, 20.3; head length, 6.9; head width, 7.3; diameter of tympanum, 1.4; diameter of eye, 3.0; naris to eye, 2.0; femur, 7.6; tibia, 8.3; fourth toe, 7.3; ratio of tibia/snout-vent length, 40.9. Head width greater than head length; snout truncate with nares conspicuous at anterior end of canthus rostralis; diameter of eye greater than distance from naris to anterior corner of eye; interorbital space 2.8, slightly less than diameter of eye; diameter of tympanum much less than diameter of eye, distance from tympanum to eye equal to about three-quarters diameter of tympanum. Digital discs present, that of digit three the largest and equal to about three-quarters area of tympanum. Fingers moderate in length, unwebbed, 3–4–2–1 in order of decreasing length; subarticular tubercles well developed, dark gray. Toes moderate in length, unwebbed, 4–3–5–2–1 in order of decreasing length, subarticular tubercles dark gray and prominent. Heels touch when femora are held at right angles to body axis. Dorsum very finely warty, warts most prominent on upper eyelids and upper surface of hindlimbs; a faint, fine, raised line from snout to above vent. Throat and belly granular; vocal sac present, large, extending posteriorly to between forelimbs, heavily glandular. Inguinal glands absent. Posterior surfaces of thighs with large, rounded, juxtaposed granules. Tongue small, oval, entire, free behind, its greatest width about one-half that of floor of mouth. Vomerine teeth in two oblique patches, beginning

[1] From the Greek *melas*, black, and *trigonon*, triangle.

well within the median border of the choanae, and separated from the choanae by a distance equal to twice the diameter of a choana, and from each other by a distance equal to slightly more than the length of one tooth row.

Coloration of type in life. Dorsal ground color medium tan with a black interocular bar, a black scapular X, its two anterior arms forming with the interocular bar a slightly darker occipital triangle; a dark gray pair of dorsolateral lines and two rather diffuse sacral spots; the two dorsolateral lines broken up posteriorly to form a series of three or four dark dorsolateral spots which approach the vent, forming a dark gray V above it; sides tan, heavily dotted with dark gray. Hindlimbs tan with two faint crossbars on the thigh, neither especially prominent and neither outlined with pale color; a more conspicuous crural crossbar, vaguely outlined with pale color; and a single dark crossbar indicated on the pes. Forelimbs with one antebrachial and one wrist bar. A prominent dark brown bar from the snout through the eye to the forelimb insertion and covering the upper half of the tympanum. Ventral ground color pinkish with some dark gray stippling, especially on the yellow vocal sac and undersides of limbs. Iris silvery above.

Variation. Variations in measurements and ratios are shown in Table III (p. 382). The vomerine series are widely separated and vary in angulation from almost straight to oblique, with the latter the more common condition.

Three of the paratypes have median dorsal pale hairlines which were creamy in life; all have some sort of dorsolateral dark markings, even if the dorsal ground color is dark brown, which separate the dorsal color from the lateral dotting or spotting. The interocular bar, scapular X and sacral spots are common features, although the latter is often almost completely obscured by the dark dorsal pigmentation. The black to dark brown postanal triangle is always conspicuous, and the leg and arm bars are likewise bold, and at times even outlined with pale color. The ventral ground color was pinkish in life, with rather uniform dark brown stippling which never formed ventral blotches or mottling. No specimen shows any indication of the pale dorsum and asymmetrical dark patches of the other two subspecies, although presumably this condition occurs.

Comparisons. E. a. melatrigonum is intermediate between *a. audanti* and *a. notidodes* in all measurements except that of tympanum diameter. The ratio of tibia/snout-vent length is likewise intermediate. The localities whence *a. melatrigonum* is known are, of course, not intermediate between those of *a. audanti* and

a. notidodes. In both dorsal and ventral pigmentation and pattern, *a. melatrigonum* resembles *a. notidodes* more closely than *a. audanti.* The hindlimb bars of *a. melatrigonum* are slightly more prominent than those of *a. notidodes,* and slightly less prominent than those of *a. audanti.* No *a. melatrigonum* has the venter blotched, as is usually the case in *a. audanti.* As noted above, there are no specimens of *a. melatrigonum* available at present showing the pale dorsum with asymmetrical blotching which occurs in both *a. audanti* and *a. notidodes.*

From *E. abbotti,* with which *E. a. melatrigonum* occurs, the latter can be best distinguished by its prominent postanal triangle and more conspicuously banded limbs. Male *melatrigonum* reach a larger size than do male *abbotti.* All measurements overlap, at times rather widely; the measurement with least overlap is that of the tibia (8.5–9.3 in upland *abbotti,* 7.8–8.5 in *a. melatrigonum*). The ratio of tibia/snout-vent length averages less in *a. melatrigonum* (45.0) than in *abbotti* (47.9), although the extremes overlap. Lower ratios are consistently those of *a. melatrigonum* (40.9–47.4), while higher ratios are those of upland *abbotti* (45.5–51.1).

Remarks. The discovery of two subspecies of *E. audanti* outside the La Selle-La Hotte massif in southern Haiti indicates that this species probably occurs throughout the higher mountains of much of the República Dominicana. The Sierra de Neiba appears to be a favored haven for high-mountain south island species which have been able to cross the Cul-de-Sac–Valle de Neiba plain, or to cross the intervening strait when the plain was flooded. In addition to *E. audanti, E. parabates* (which is a north island representative of the south island *E. ventrilineatus-E. jugans* group) is another species of frog which has distinctly south island affinities, and occurs only in the Sierra de Neiba. *E. audanti,* on the other hand, has been able to extend its range farther north into the Cordillera Central, and in so doing has been able to cross the rather xeric but high Valle de San Juan. It is likely that *E. audanti* occurs in the central Haitian mountains as well, since these are continuous with the Dominican Sierra de Neiba and Cordillera Central; the Haitian mountains are very poorly known herpetologically. It is, of course, possible that *audanti* is a north island species, having evolved in the uplands of the Cordillera, and thence expanded southward into the Sierra de Neiba, across the Cul-de-Sac into the Massif de la Selle and thence into the Massif de la Hotte. Neither explanation is better substantiated than the other.

FIG. 2. Hispaniola, showing the known distribution of *E. abbotti* (solid circles) and *E. audanti* (open circles); semi-solid circles represent localities whence both species have been taken. Semi-solid circles in the Sierra de Neiba represent localities for *E. abbotti* and *E. audanti notidodes*; semi-solid circles in the Cordillera Central represent localities for *E. abbotti* and *E. audanti melatrigonum*.

ELEUTHERODACTYLUS MINUTUS AND *ELEUTHERODACTYLUS HAITIANUS*

These two species present an even knottier problem than do *E. abbotti* and *E. audanti*. Regarded by Cochran as two distinct species, *minutus* and *haitianus* are both known only from the Cordillera Central in the República Dominicana. Both seem to be small forms, with *haitianus* the smaller (but see further comments below). Shreve and Williams (1963: 322) regarded *haitianus* as a synonym of the prior *minutus*, and the latter as possibly an upland subspecies of *abbotti*. Cochran (1941: 26) considered that *minutus* had a smooth belly (and was in fact following Noble, 1923: 4, in his original diagnosis of *minutus*) and *haitianus* (= *intermedius*, *sensu* Cochran) had a granular belly. Her figures (pp. 47, 70) show that *minutus* is a rather long-legged species, reaching a known snout-vent length of 18 mm, and that *haitianus* is distinctly short-legged, reaching a known snout-vent length (in the type) of 21 mm. Cochran also commented in the text (1941: 48) that the "paratype" of *minutus* which she examined had a slightly granular belly. Shreve and Williams (1963: 323) later noted that the venter of *minutus* is coarsely granular, in contrast to the more finely granular venters of *abbotti* and *audanti*.

Perhaps the best way to unravel this complicated situation is to discuss the field situation, based on my recent collections only, and then turn to the nomenclatorial problems. In the Cordillera Central, primarily to the north of Constanza and between that town and El Río, there occurs a small frog with a maximum snout-vent length of 17.0 mm in males and 19.4 mm in females. This *Eleutherodactylus* is thus smaller in both sexes than *abbotti*, and males are smaller than male *audanti melatrigonum* from the same general area. The species occurs from 3600 to 6100 feet, in upland broadleaf forests; males call from herbaceous plants, often terrestrial bromeliads, not more than one foot above the ground surface. The call is a single, rising, high-pitched "wheep," almost a pulse, very faint and insect-like. The dorsal ground color varies from tan to brown, with darker sides, and occasionally there are reddish dorsolateral lines separating the dorsal and lateral colors. The dark postanal triangle is fairly distinct, the legs are banded, but rather inconspicuously so at times, and there are remnants of a scapular X. All dorsal pattern elements have a distinctly "muddy" appearance, with no feature being especially clear-cut or prominent (Fig. 3, left). Ventrally, the ground color varies from very pale yellow or cream to gray, and the belly may be either immaculate or have some dark gray dots scattered over it. In addition to the

scapular X, there may be a sacral chevron or smudge; the forelimbs are usually somewhat reddish orange.

To the southeast of Constanza, centering in the high Valle Nuevo region, there occurs a small frog with a maximum snout-vent length of 14.8 mm in males and 16.6 mm in females. This species occurs from 5600 to 8000 feet, mainly in pine woods, where it has been found under rocks and logs, and under sheets of moss along a road cut. One calling male was taken about ten inches above the ground on a herbaceous leaf near a small pool in the woods. The call is a descending scale of staccato "beeps." The dorsal ground color varies from tan to very dark brown, almost black in many cases; the brachium is pale reddish, and the ankle often has a reddish brown hue. The dorsal pattern consists of a

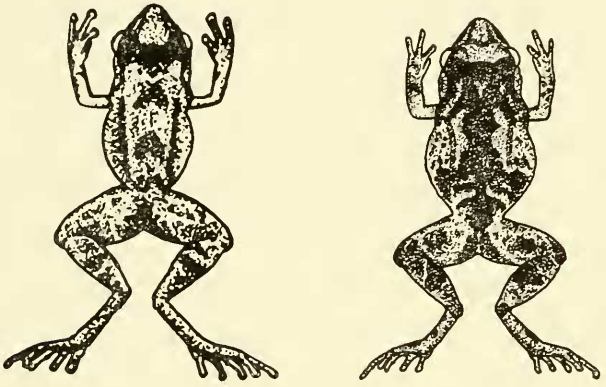

FIG. 3. *Left: Eleutherodactylus minutus*, adult female, ASFS X8938, 16 km N Constanza, 6000′, La Vega Province, República Dominicana; snout-vent length 19.4 mm.
Right: Eleutherodactylus haitianus, adult male, ASFS X8392, 9 km NNE Valle Nuevo, La Vega Province, República Dominicana; snout-vent length 13.9 mm.

band usually outlined in dark brown to black, occasionally with a median pale hairline. A common variant is the "dead leaf" pattern — a series of obliterative pale and dark dorsal areas which render the frog inconspicuous against a varicolored brown background. The snout is usually pale and sharply set off from the balance of the back. A series of four dark lateral bars, radiating from the sacrum, is commonplace (Fig. 3, right). The ventral ground color varies from pale yellow (especially on the vocal sac

in males) to clear white (not gray), and the belly and throat are very heavily spotted with rather large dark brown to black spots in almost all specimens. All dorsal pattern elements are sharp and distinct, including the hindlimb bands which are usually outlined with tan and stand out boldly from the ground color. There is a dark postanal triangle which may be distinct or inconspicuous, depending upon the intensity of the dorsal ground color.

The two forms are almost completely separable on the tibia/snout-vent length ratio. The larger form from north of Constanza averages 46.0 (44.5–49.7) in males and 47.3 (43.9–53.1) in females, whereas the smaller, more southern form averages 41.3 (37.2–45.0) in males and 40.4 (36.1–43.3) in females.

When all aspects of these frogs are considered — the coloration and pattern, morphology, habitat, altitudinal distribution, and vocalization — there seems little doubt that we are dealing with two distinct species.

The nomenclatorial problems involved in allocating names to them are somewhat more complex. I have examined the type of *E. minutus*, but not that of *haitianus*; the latter is, however, well illustrated by Cochran and some pertinent measurements are given. I have had access to the large series of paratypes of *haitianus* and these, although helpful, are so confusing in many ways that they require special discussion.

The type locality of *E. minutus* is "near Paso Bajito, Jarabacoa-Constanza Trail"; Paso Bajito is to the north of Constanza. The elevation is not excessively high; we estimate it at about 4000 feet.

The type of *minutus* (AMNH 11404) is a gravid female with a snout-vent length of 17.3 mm and a tibia length of 8.0 mm. The frog is presently much faded, but dorsally there is a pale zone with a faint scapular X and a faint sacral chevron, distinctly darker sides, only the vaguest indications of leg bars and an interocular bar, and a pale belly with very slightly darker spotting. Of the two species discussed above, the type of *minutus* agrees best with the larger form, which occurs to the north of Constanza, in pattern and size. Additionally, the tibia/snout-vent length ratio in the type (46.2) falls within the extremes of this ratio in the larger of the two species (females, 43.9–53.1), and not within this ratio in the smaller (females, 36.1–43.3). One other factor needs consideration: Noble (1923: 4) described the belly of *minutus* as smooth. Examination of the type of *minutus* shows that the belly is, in fact, rather faintly granular; in this, again, it agrees with the larger of the two species discussed above. (Both the species under discussion have granular bellies; that of the smaller species is more

coarsely and heavily granular than that of the larger.) In consideration of the above data, I have no hesitancy in assigning the larger species of frog, described in detail above, to *minutus*.

There remains the possibility, suggested by Shreve and Williams, that *minutus* is an upland race of *abbotti*. Against this suggestion is the fact that the two, although similar in pattern, are quite different in intensity of dorsal pigmentation and in size (largest upland *abbotti* male 18.9, female 25.4; largest *minutus* male 17.0, female 19.4). Vocally they are distinct. Finally, they occur together at two of our recent localities (9.1 miles north of Constanza; 3.3 miles east of El Río), and very close together at another (9.3 miles north of Constanza), where *abbotti* was taken at 6000 feet, *minutus* at 5600 feet. There is no evidence of intermediate specimens, although admittedly intergrades might be extremely difficult to differentiate from the parent populations. Certainly, however, when *minutus* and *abbotti* are collected at the same locality, there is no difficulty in distinguishing one from the other. The tibia/snout-vent length ratio of the two overlaps in both sexes. The means are, however, higher in *abbotti*, averaging 47.9 (45.0–51.1) in males, 48.9 (45.6–51.3) in females; male *minutus* average 46.0 (44.5–49.7), females 47.2 (43.9–53.1).

Turning now to the southern small frogs from the Valle Nuevo region, it would seem quite logical to assume that these specimens are *haitianus*. The type locality, Loma Rucilla, lies about 23.3 miles to the northwest of Valle Nuevo, and the elevation of the type and Loma Rucilla paratypes is expressly stated as 8000 to 10,000 feet. There are three lots of paratypes: USNM 107567, 107569–74, MCZ 23469–74 (17 specimens), Loma Rucilla; USNM 107575–76, Loma Vieja; USNM 107578–85, MCZ 23495–500 (27 specimens), Valle Nuevo. The two paratypes from Loma Vieja are clearly *minutus* in size, pattern, and tibia/snout-vent length ratio, and need not be further considered. Ten of the 35 "*haitianus*" from Valle Nuevo are also *minutus*; if they are actually from Valle Nuevo itself, they represent a new altitude record for *minutus* of 7600 feet. However, the paratypic series is labeled as coming from 6000 to 8000 feet, so that the *minutus* may have come from within the known altitudinal limits of that species.

Twenty-four of the Valle Nuevo paratypes are like the recent Valle Nuevo material discussed above, and are remarkable only in that the series contains females (up to 18.0 snout-vent) and males (up to 15.8) which are larger than the more recently taken specimens. The remaining paratype, a male, has a broad, pale middorsal stripe, a feature not observed in the fresh specimens.

The twenty-four paratopotypes from Loma Rucilla are extremely puzzling. The type specimen was recorded by Cochran (1941: 71) to have a snout-vent length of 21, and thus exceeds all Valle Nuevo specimens in size. Among the paratypes are large females with snout-vent lengths from 18.0 to 19.7, bridging the gap in size between the largest female from Valle Nuevo and the holotype. One of the six males (USNM 107572) is clearly *E. minutus* (thus apparently raising the upper altitudinal limit of that species to at least 8000 feet). Of the five remaining males, four are small and the fifth very large (snout-vent 17.5), in fact larger than any other male.

Loma Rucilla frogs lack the heavily spotted venters of the Valle Nuevo frogs, and have throats which are dark with some paler flecking. The larger frogs have unmarked venters and dark throats, the smaller ones spotted venters; the latter group approximates the recently collected material from Valle Nuevo, although the frogs are larger and have less ventral spotting. Cochran's description of the type, "ventral surfaces . . . clouded with minute darker dots," her drawing of the specimen, and its size agree with the larger Loma Rucilla frogs in detail.

The nomenclatorial problem resolves itself into how many forms (species or subspecies, if any) are involved. It seems rather unusual, for example, that there should be such a large difference in size in adult females between Valle Nuevo and Loma Rucilla. None of the female Valle Nuevo specimens is equal in size to the type or to the larger of the female paratypes from Loma Rucilla. The difference in size, correlated with a difference in ventral pigmentation, noted among the Loma Rucilla specimens, strongly suggests that we may be dealing with two species of frogs (the larger species, *E. haitianus*). Aside from the ventral pigmentation and size, I am unable to differentiate these two "forms" from one another. The tibia/snout-vent length ratio of the larger specimens falls neatly within the extremes of this ratio in specimens from Valle Nuevo. The teeth appear identical, and there are no external characteristics which differentiate them when preserved. Interestingly, a single gravid female (MCZ 40813) from Paraje La Ciénaga, Manabao, in La Vega Province, has a snout-vent length of only 14.7, and is clearly much more like the Valle Nuevo frogs than the larger Loma Rucilla frogs. La Ciénaga lies about 7 miles east of the peak of Loma Rucilla. This single small female suggests very strongly that the larger Loma Rucilla specimens actually are specifically distinct from the more southern frogs.

Another possibility is that there are two subspecies of *E. haitianus* involved, one on Loma Rucilla and the other to the south and east, the Loma Rucilla frogs characterized by larger size and much less heavily pigmented venters. Living specimens may be very distinct, since many colors are evanescent in *Eleutherodactylus*. The least likely solution is that the presumed differences in ventral pigmentation and size are happenstance artifacts of collecting; the large number of specimens from both Valle Nuevo and Loma Rucilla makes this very unlikely.

Without further data in life on the Loma Rucilla populations, there seems only one course open, that of regarding all these frogs as *E. haitianus*, while acknowledging rather important differences between the northern and southern populations.

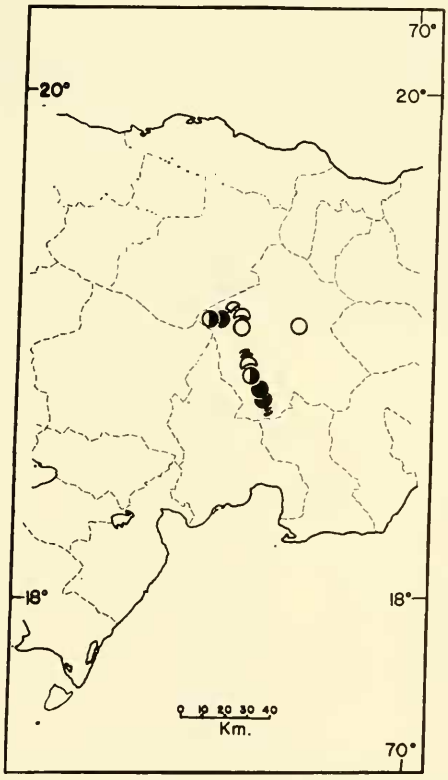

FIG. 4. Central República Dominicana, showing localities for *E. minutus* (open circles) and *E. haitianus* (solid circles). Semi-solid circles represent localities whence both species have been taken.

There is no question that *E. haitianus* is distinct from *E. minutus*. Aside from the habitat and vocal differences discussed above, the two species are easily differentiated on the basis of the tibia/snout-vent ratio; this and other meristic characters are shown in Table IV. That the two species apparently occur together is based entirely on old material with possibly less accurate and carefully taken data than we have for more recently collected specimens; in our experience they do not occur at precisely the same localities. This is also true for the upper altitudinal limits of *minutus*; all the higher elevations are based on old material. Until the older data can be confirmed, it seems appropriate to regard *minutus* as having a lower altitudinal distribution than *haitianus*, although there is an overlap of 500 feet, according to freshly taken and carefully documented material (see Fig. 4 for distribution). There is a need for rather precise notation of elevation in the Cordillera Central. A hike covering several thousand feet elevation may well encompass the altitudinal limits of several species of frogs; the issue may become quickly clouded if all specimens are labeled as coming from between the two extremes in elevation without due regard for more precise altitude.

TABLE IV. Means and extremes of *E. minutus* and *E. haitianus*. For *haitianus* the ten largest of each sex from the Valle Nuevo region were used; for *minutus* all adults of each sex. (Tibia/snout-vent ratio computed for all specimens of each sex from Valle Nuevo, regardless of maturity.)

	E. minutus	*E. haitianus*
	8♂	10♂
snout-vent length	16.4 (15.5–17.0)	13.5 (12.5–14.8)
head length	5.8 (5.5– 6.1)	4.7 (4.4– 5.0)
head width	5.6 (5.3– 6.0)	4.6 (4.2– 5.0)
tympanum	1.0 (0.9– 1.3)	0.9 (0.8– 1.3)
eye	2.2 (2.1– 2.4)	1.9 (1.7– 2.0)
naris to eye	1.4 (1.2– 1.5)	1.1 (1.0– 1.3)
femur	6.6 (6.3– 7.1)	5.1 (4.8– 5.6)
tibia	7.5 (7.3– 7.7)	5.5 (5.0– 5.7)
fourth toe	6.5 (5.8– 6.8)	4.9 (4.5– 5.6)
tibia/snout-vent ratio	46.0 (44.5–49.7)	41.3 (37.2–45.0)
	7♀	10♀
snout-vent length	17.9 (16.0–19.4)	14.8 (12.0–16.6)
head length	6.4 (5.9– 6.9)	5.1 (4.7– 5.8)
head width	6.1 (5.5– 6.6)	5.0 (4.2– 5.6)
tympanum	1.1 (1.0– 1.4)	1.1 (0.7– 1.2)
eye	2.4 (2.1– 2.6)	1.9 (1.7– 2.2)
naris to eye	1.5 (1.3– 1.8)	1.3 (1.1– 1.5)
femur	7.6 (6.9– 8.0)	5.6 (4.7– 6.0)
tibia	8.5 (7.9– 8.8)	5.9 (5.5– 6.5)
fourth toe	7.2 (5.7– 7.7)	5.2 (4.8– 5.7)
tibia/snout-vent ratio	47.3 (43.9–53.1)	40.4 (36.1–43.3)

E. haitianus has not been collected with *E. audanti*. Our collections also indicate that *haitianus* and *abbotti* do not occur together, although the altitudinal ranges of the two overlap by 400 feet. There are specimens of *haitianus* and *abbotti* from Loma Rucilla, the latter from an elevation of 6000 feet. The two species can be separated by the much shorter tibia of *haitianus* and the larger size of *abbotti*. The tibia/snout-vent length ratios of these two species in the Cordillera uplands are: male *haitianus* 41.3 (37.2–45.0), male *abbotti* 47.9 (45.5–51.1), female *haitianus* 40.4 (36.1–43.3), female *abbotti* 48.9 (45.6–51.3).

There are four other small *Eleutherodactylus* specimens from the Cordillera Central which are of interest. These are two males and one female from 11 km (6.4 miles) east of Paso Bajito, 4500 feet (ASFS X8839–41), and a female from Valle Nuevo (MCZ 23498). The two males are in some ways very like *E. abbotti*, except that they are distinctly longer-legged than any male montane *abbotti* (tibia/snout-vent length 55.9 and 54.1). They also appear to be more broad headed. Both have leg bars of the *abbotti* style, and an inconspicuous postanal triangle like *abbotti*. They differ from *abbotti* in ventral pigmentation, since both have a series of dark spots along the lower jaw, and additionally one has some dark ventral dotting. Of the females, one is gravid and has a snout-vent length of 18.1, which is rather small for gravid *abbotti*. These two frogs, from two widely separated localities (MCZ 23498 is a paratype of *haitianus*), are very similar dorsally in that the pattern consists of a pale snout, a very dark chestnut triangle from the interocular bar onto the sacrum where it meets, apex to apex, with another triangle which has its base across the groin. The ground color is a dull orange-tan. There is a prominent postanal triangle, but no other hindlimb markings except dark ankles. Ventrally, these frogs have some faint stippling on the throat and a series of dark spots along the lower jaw margin. Whether these two females are correctly associated with the two males above is unknown. At least the Paso Bajito female has a tibia/snout-vent length ratio of 48.1, a figure which is included within the known range of Cordillera *abbotti*. The Valle Nuevo female, on the other hand, has a ratio of 40.0, which is far below all Cordillera *abbotti* females, and within the extremes of female *haitianus*, a species with which it is definitely not associated.

I have not assigned any of the above four specimens to any species. They may represent one or two new species of small Cordilleran frogs, or they may be aberrantly long-legged or pigmented individuals of well-known upland species.

RELATIONSHIPS OF SMALL HISPANIOLAN FROGS

Of the four species discussed in the present paper, three are clearly members of the *auriculatus* group — i.e., *E. abbotti, E. audanti,* and *E. minutus.* As in other members of the group, the presence of a granular venter, enlarged digital discs, short patch-like vomerine series, and an external vocal sac indicate their affinities. *E. haitianus* probably should likewise be considered a member of this assemblage. It differs from the others in having much smaller digital discs and a somewhat more squatty habitus. All four species lack inguinal glands; all four have the peritoneal covering of the testes completely pigmented with jet black chromatophores, while the peritoneal covering of the ovaries has scattered black to gray chromatophores. This dark gonadal pigmentation is a phenomenon which occurs sporadically in Antillean *Eleutherodactylus,* without apparent regard for the affinities of the species. For instance, it occurs in the *dimidiatus* group (*jugans, parabates, ventrilineatus*), in the *ricordi* group (*zugi*), as well as in the *auriculatus* group.

There is a possibility that *E. haitianus* should be assigned to the *varleyi* group, in which are presently included (Shreve and Williams, 1963: 339): *varleyi, glanduliferoides,* and *cubanus. E. glanduliferoides* and *varleyi,* in addition to having the *varleyi* group characters of feebly developed discs, short vomerine series, and small size, also have prominent inguinal and popliteal glands; Shreve and Williams commented that *varleyi* did not possess these structures, but they are prominent and orange colored in freshly collected material. I do not know if *cubanus* possesses glands. *E. varleyi* has a pectoral vocal sac; the condition of the vocal sac is unknown in *glanduliferoides,* and *cubanus* apparently lacks a vocal sac. *E. cubanus* and *glanduliferoides* are smooth ventrally; *varleyi* was diagnosed as having a granular belly, although the specimens before me appear to have smooth venters.

E. haitianus resembles the *varleyi* group members in small size, pattern, and short vomerine series. However, the venter is coarsely granular, there are no inguinal or femoral glands, and there is a vocal sac. Black testes are not found in the species *varleyi,* at least. On the basis of all characters, I prefer to regard *haitianus* as a member of the *auriculatus* group, somewhat more divergent than its near relatives in the Cordillera.

Of the four species involved in the present discussion, *abbotti* and *audanti* are more closely related to one another than to *minutus* and *haitianus.* Likewise, *minutus* and *haitianus* are more closely related, with *minutus* more like the *abbotti-audanti* pair.

As noted before, *audanti* is presumably an upland derivative of *abbotti* (which is widespread throughout the island); *audanti* has either evolved in the Massif de la Selle and migrated thence to the La Hotte, on the one hand, and to the Sierra de Neiba-Cordillera Central, on the other, or has evolved in the Cordillera and has moved thence south into the La Selle. More mesic conditions in the lowlands would have facilitated such movement. Both *minutus* and *haitianus*, occurring, as far as is known, only in the Cordillera, may well represent a sequential series *abbotti-minutus-haitianus* (if *audanti* was not developed from *abbotti* in the Cordillera but is an immigrant there), or *abbotti-audanti-minutus-haitianus* (if *audanti* developed in the Cordillera and is an immigrant to the La Selle).

Specimens examined

Eleutherodactylus abbotti: *Haiti, Dépt. du Sud,* ASFS X2797, X2917–22, Camp Perrin; ASFS X3347–51, Carrefour Canon, 500′; MCZ 37729, Marfranc; *Dépt. de l'Ouest,* ASFS X1363–80, X2006–08, X2011, Peneau, 5000′; ASFS X1649, X1795–812, X1818, X1899, MCZ 33546–50, 33552–60, 33562–63, 33565, 33568–73, 33576–79, 33581, 33586–87, 34212, 34221, 34223, 34226, 34229, 34231–32, 34234, 34242–46, 34249, 34250–53, 34256, 34258, 34261–62, 34264, 34272, 34275–76, 34278–81, 34283–84, 34287–89, 34291–92, 34295, 34301–02, 34304–05, + 16 unnumbered specimens, 31729, 31730–32, 31797, Furcy, 5600′; ASFS X3868–69, 2.4 mi. S Kenscoff; MCZ 33280, Morne de Cayette; MCZ 36742, Thiotte; MCZ 31952–53, Savane Zombi, Forêt des Pins; *Dépt. du Nord,* MCZ 3100, 3526, Grande Rivière du Nord. *República Dominicana, Barahona Prov.,* ASFS X9642–43, 3.3 mi. NE La Ciénaga; ASFS X9791–94, 0.6 mi. N Las Auyamas, 3000′; ASFS X9809–15, 1.8 mi. N Las Auyamas, 3400′; ASFS X9914–15, 8 km NE Las Auyamas, 2600′; ASFS X9919, V71–83, 10.5 mi. S Cabral, 3500′; ASFS V152, 24 km SW Barahona, 3700′; MCZ 35779–90, del Monte's finca, nr. Barahona; MCZ 35791–96, Herrmann's finca, nr. Paraíso; *Dajabón Prov.,* ASFS V1623–24, 12 km S Loma de Cabrera, 2400′; *Valverde Prov.,* ASFS V1241, 9 km N La Cruz de Guayacanes, 1600′; *Puerto Plata Prov.,* ASFS V1689, 8 km E Imbert, 1100′; MCZ 23545–46, 25 km S Puerto Plata; *Santiago Prov.,* MCZ 23451–55 (8 specimens), Pico Diego de Ocampo; *Espaillat Prov.,* ASFS V1698, 6 km SE Sabaneta de Yásica; ASFS V1955, 2 km N Puesto Grande, 2200′; *María Trinidad Sánchez Prov.,* ASFS V1860, 2 km S El Factor; *Samaná Prov.,* ASFS

V1914, 11 km E Sánchez; MCZ 23530–31, Sánchez; ASFS V1976–82, 5 km W Samaná; *Duarte Prov.*, ASFS V1823–24, 9 km NW Pimentel; *El Seibo Prov.*, ASFS X7835–36, X7975–81, 3.5 mi. S Sabana de la Mar; ASFS X7902–07, 3.3 mi. SW Miches; ASFS X9267, 2.3 mi. SE Miches; ASFS X9337, 1.4 mi. SE Miches; *La Vega Prov.*, ASFS X8564–601, X8880–84, 4 km SW El Río, 4000′; ASFS X8116, 11.5 mi. E El Río, 3800′; ASFS X9162–63, 23 km E El Río, 3050′; ASFS X9197–98, X9225–32, X9240, 6 km E El Río, 3600′; ASFS V1735, 14 km SW La Vega, 1600′; ASFS V1792, 4 km NW La Vega; ASFS V2021, 12 km NE Jarabacoa, 2000′; MCZ 40812, Paraje La Ciénaga, Manabao, Municipio Jarabacoa; MCZ 31129, 40815–18, Constanza; ASFS X8249–54, 1 mi. S Constanza, 4000′; ASFS X8244–48, 7.2 mi. S Constanza, 5000′; ASFS X9085, 11.5 mi. SE Constanza, 5800′; MCZ 23520–21, Loma Vieja, 6000′; ASFS X8754–64, 5.1 mi. N Constanza, Valle de Culata, 5000′; MCZ 40811, La Ciénaga, Culata; MCZ 30588, Aserradero Bermúdez, Constanza; ASFS X9796, 9.1 mi. N Constanza, 6000′; ASFS X8949, 16 km N Constanza, 6000′; ASFS X8826, X8829–30, 6 km W. Constanza, 4250′; ASFS X8892, X8897, Tireo Abajo; MCZ 40806, 43458–65, La Palma, Constanza; MCZ 23481–82, Loma Rucilla; ASFS X8126–27, 1.2 mi. SE Monseñor Nouel, 700′; *San Rafael Prov.*, MCZ 31170–71, 40814, Rancho de la Guardia; ASFS V380–84, 14.5 km SW Hondo Valle, 4750′; ASFS V532, V536, 25 km S Elías Piña, 5000′; ASFS V537, 19 km S Elías Piña, 4000′; ASFS V543–46, 15 km S Elías Piña, 3400′; *San Juan Prov.*, ASFS V393, 7 km W Vallejuelo, 2600′.

Eleutherodactylus audanti audanti: *Haiti, Dépt. du Sud,* MCZ 21551–53, foothills, Massif de la Hotte; *Dépt. de l'Ouest,* MCZ 34208–11, 34213–20, 34222, 34224–25, 34227–28, 34230, 34233, 34235–41, 34247–48, 34254–55, 34257, 34259–60, 34263, 34265–71, 34273–74, 34277, 34282, 34285–86, 34290, 34296–300, 34303, 34306–07, + 33 unnumbered specimens, 33551, 33561, 33564, 33566–67, 33574–75, 33580, 33582–85, 37728, ASFS X1813–17, X1819–98, X1900–02, Furcy, 5600′; ASFS X1362, X2009–10, X2012–13, Peneau, 5000′; ASFS X1313–21, 2.5 mi. S Kenscoff, 5600′; ASFS X2362–64, X3870–72, 2.4 mi. S Kenscoff; MCZ 24280 (5 specimens), USNM 72595–97, Morne Cabaio, 7000′; MCZ 21576–89 + 39 unnumbered specimens, La Visite, La Selle range; MCZ 19704–08, USNM 95111–13, Mont la Selle; USNM 85009, "Morne la Selle"; ASFS X1922, X3920–27, Forêt des Pins, 5800′; MCZ 31954–63, Marie Claire, Forêt des Pins; MCZ 24586–88, Bois Pin, nr. Marigot.

Eleutherodactylus audanti melatrigonum: *República Dominicana, La Vega Prov.*, MCZ 43206, ASFS X8773, X8775–77, 7 km N Constanza; AMNH 71993–96, 5.1 mi. N Constanza, 5000′.

Eleutherodactylus audanti notidodes: República Dominicana, San Rafael Prov., MCZ 43204, ASFS V372–74, AMNH 71990–92, 20 km SW Hondo Valle, 5950′; ASFS V385, 14.5 km SW Hondo Valle, 4750′; MCZ 43205, 25 km S Elías Piña, 5000′.

Eleutherodactylus haitianus: *República Dominicana, La Vega Prov.*, USNM 107567, 107569–71, 107573–74, Loma Rucilla, 4000–10000′; MCZ 23469–74 + 11 untagged specimens, Loma Rucilla; USNM 107578–85, Valle Nuevo, 6000–8000′; MCZ 23499–500 + 14 untagged specimens, 31588–89, Valle Nuevo; MCZ 40813, Paraje La Ciénaga, Manabao, Municipio Jarabacoa; ASFS X8294–99, X8465, 9 km NE Valle Nuevo, 7400′; ASFS X8392–94, 9 km NNE Valle Nuevo; ASFS X8339–40, 3 km NNE Valle Nuevo; ASFS X8461–62, 11 km SE Valle Nuevo, 8000′; ASFS X8994, 5.3 mi. SE Valle Nuevo, 8000′; ASFS X9070–76, 8.4 mi. SE Valle Nuevo, 7900′; ASFS X8676, 8.9 mi. SE Valle Nuevo, 8000′; ASFS X9083, 15 km SE Constanza; ASFS X8929, 16 km SE Constanza, 5600′; ASFS X9153, 11.8 mi. SE Constanza, 5800′.

Eleutherodactylus minutus: *República Dominicana, La Vega Prov.*, USNM 107572, Loma Rucilla, 4000–7000′; AMNH 11404, MCZ 9338, Paso Bajito; ASFS X9241, 12 km E El Río, 3600′; ASFS X8713, X8795, 9.1 mi. N Constanza, 6000′; ASFS X8790, X8938–47, 16 km N Constanza, 6000′; ASFS X9145, 12.6 mi. SE Constanza, 6100′; USNM 107575–76, Loma Vieja, 6000′; MCZ 23495–97 + 6 untagged specimens, Valle Nuevo.

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